Kin recognition

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Kin recognition: function and mechanism in avian societies

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Cooperative behaviour resulting from kin selection is widespread among animals and the ability to recognize and discriminate between kin and non-kin is a critical element in kin selection theory. Current evidence suggests that associative learning is the most likely mechanism of kin discrimination. However, surprisingly, there have been no experimental studies of the putative 'associative-learning period', the likely recognition mechanisms enabling fine discrimination between close and distant kin of similar familiarity, whether generic or individual cues are employed in kin recognition, and how recognition ability varies at different stages of a species' life history. Comparative studies of kin recognition and discrimination in cooperative and noncooperative species are also needed to shed light on the adaptive value of helping behaviour and to identify key factors in the evolution of cooperation.

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In many cooperatively breeding birds and mammals, individuals help conspecifics to produce offspring rather than have young themselves. An individual can increase its genetic representation in future generations by helping close relatives who share copies of its genes identical by descent. The role of kin selection (the selection process that enhances the fitness of close relatives through increased survival and/or increased reproductive success) is regarded as highly important for the evolution of helper systems; helpers gain most via indirect fitness by providing aid to their closest genetic relatives[1]. Therefore, the ability to recognize and discriminate between kin and non-kin is crucial for maximizing fitness. Kin discrimination through kin recognition is central to the evolution of social behaviour. For a considerable number of bird species, there is good evidence for preferential allocation of aid to closest kin[2] (Box 1). However, helping behaviour might also evolve and be maintained in the absence of kinship through, for example, the gain of future direct benefits (e.g. breeding experience and territory inheritance). For example, helpers in red-cockaded woodpeckers (*Picoides borealis*)[3] and stripe-backed wrens (*Campylorhynchus nuchalis*)[4] did not alter their feeding rates when provisioning full- versus half-sib offspring. Male wrens that help their stepmother to rear half-sibs profit by breeding with her when their father dies[5]. Although there is good evidence for kin discrimination, and the ability to recognize kin has been subject to detailed examination in noncooperative species, the fitness consequences of kin recognition have rarely been documented[6]. Here, we evaluate experimental evidence for kin discrimination and discuss the mechanisms and adaptive value of kin recognition in cooperatively breeding avian societies.

Experimental evidence for kin-directed care

Most experimental studies of kin-directed care among birds have dealt with parent–offspring recognition in monogamous birds, examining either the ability of parents to recognize their own young, or the ability of young to recognize their parents. In general, three types of discrimination tests have been used to test offspring–parent recognition: (1) choice tests between two loud-speakers simultaneously playing recorded calls of own and unrelated unfamiliar individuals; (2) sequential discrimination tests (swapping own brood for an unfamiliar brood of the same age); and (3) auditory tests to examine the parents' ability to recognize and locate their young when moved from the nest site. In most species, it seems that parents and offspring do recognize each other. However, care is required in drawing firm conclusions.

One shortcoming is that the presence of kin discrimination and the types of cue used for kin recognition have often been tested using one method of experiment only, whereas other experimental designs can generate different results. For example, parents of bank swallows (*Riparia riparia*) use only visual cues to recognize their offspring[7]. If the parents are simultaneously played recorded begging calls (auditory cues) of their own offspring with those of offspring of the closely related rough-winged swallow (*Stelgidopteryx serripennis*), bank-swallow parents fail to recognize the calls of their own offspring[7]. However, cross-fostering experiments showed that bank swallows discriminate visually between their own offspring and those of rough-winged swallow[7] (Box 1).

A second shortcoming of discrimination tests is that the outcome is often inconclusive. For instance, an experiment on adelie penguin (*Pygoscelis adeliae*) showed that parents peck at young that are not their own[8]. This behaviour could be interpreted as offspring recognition, but it could also arise through parent recognition if fostered offspring behave strangely towards foster parents.

A third limitation of discrimination tests concerns the type of test used. If parents recognize their young through a simple rule 'feed anything in my nest', then in sequential discrimination tests they should still feed the foster chicks in their nest. Simultaneous cross-fostering tests, which are forced choice tests with the offspring pitted against unrelated young, are more sensitive than sequential discrimination tests[9]. A combination of simultaneous and sequential tests may reveal a more sophisticated decision rule (for example based on familiarity or true kin recognition). However, very few studies of this type (or, indeed, ones that integrate other types of tests) have been conducted (Box 1). Two studies that have integrated simultaneous and sequential tests have revealed that the ability of Caspian tern (*Sterna caspia*) parents to discriminate conspecific chicks[10], and the ability of rough-winged swallow parents to discriminate conspecific from heterospecific chicks both depend on the ecological circumstances and type of cross fostering used (e.g. swapping entire broods or part of the brood)[11,12].

Finally, we have to be careful about drawing general conclusions about kin recognition in a particular species if the species' ability to recognize kin varies with different life history stages – recognition at one stage (e.g. eggs or chicks) does not imply recognition at another.

There are few experimental studies on parent–offspring and sibling recognition for cooperatively breeding birds[13]. Given that many cooperative-breeding systems involve the acquisition of indirect fitness benefits through helping kin, there must be some recognition mechanism between kin and non-kin. Kin recognition studies offer two exciting opportunities to advance our understanding of cooperative systems. First, they will provide insight into the

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Box 1. Observational and experimental evidence for kin-directed care

Observational evidence

- When faced with a choice of potential recipient nests, helpers preferentially help the breeding pair to whom they are most closely related. This has been documented for the white-fronted bee-eater (*Merops bullockoides*)[30], Galapagos mockingbird (*Nesomimus parvulus*)[33], bell miner (*Manorina melanophrys*)[34,35], noisy miner (*M. melanocephala*, T. Pøldmaa, unpublished) and pinyon jay (*Gymnorhinus cyanocephalus*)[36]. Only one species, the Mexican jay (*Aphelocoma ultramarina*), is not reported to show kin favouritism[37].
- The indirect fitness benefit available to helpers will be relatively low when helping half-sibs (produced by a parent plus unrelated step-parent) rather than full-sibs, so care by helpers is predicted to be reduced. The evidence for this is mixed. White-fronted bee-eaters[2], Florida scrub jays (*Aphelocoma coerulescens*)[38] and Seychelles warblers (*Acrocephalus sechellensis*)[21] exhibit the predicted adjustment in helping behaviour. Each study found that the proportion of nonbreeders that helped decreased when unrelated step-parents became breeders.

Experimental evidence

- An intraspecific cross-fostering experiment in the Caspian tern (*Sterna caspia*) showed that parents will accept young substituted for their own in the first week of life. However, when given a choice between their own and alien young, in nest scrapes either side of the original nest, they will unfailingly choose their own throughout the nestling period[10]. In this species, the same results were obtained in egg-fostering experiments[39].
- Interspecific cross-fostering experiments in the rough-winged swallow (*Stelgidopteryx serripennis*) and bank swallow (*Riparia riparia*), both breeding in the same colony, showed similar results[11]. When bank swallow and rough-winged swallow broods were exchanged from adjacent burrows, both sets of parents were attracted to the calls of their own young and soon began to feed their chicks at the new locations, implying brood recognition. In addition, when a single rough-winged swallow chick was added to a bank-swallow brood, foster chicks were typically rejected, implying individual recognition. However, when a single bank-swallow chick was added to a rough-winged swallow brood, the foster chick was invariably accepted[12].

potential complexity of the rules used by individuals to recognize kin and, second, they will reveal how these rules might make sense given particular ecological circumstances.

Kin recognition mechanisms

The occurrence of facultative adjustment of provisioning effort according to relatedness among (cooperatively) breeding animals implies that some sort of mechanism must be used to achieve kin discrimination. Four categories of mechanisms have been proposed: recognition alleles, phenotype matching, recognition through association or familiarity and spatially based recognition (Box 2).

Although an attractive idea, the existence of recognition alleles among birds, or other taxa, is unlikely. First, there is no empirical evidence for recognition alleles. Second, recognized individuals might simply share recognition traits and need not be kin, so this mechanism would be vulnerable to the evolution of alleles producing the phenotypic trait but not the associated altruistic behaviour. Third, meiotic shuffling of genes (when dealing with more than one allele or gene) might also make genetic templates unreliable. Finally, there could be conflict among individuals over whether phenotypic traits that give unambiguous information on kinship are expressed[14–16].

In practice, it is probably extremely difficult to distinguish between recognition through phenotype matching and recognition alleles. Among birds, phenotype matching has been invoked to explain the mating preference of Japanese quail (*Coturnix coturnix japonica*) for first cousins[17].

A simple spatially based recognition rule, such as 'feed anything in my nest or territory', is widespread and successfully exploited by bird species that are brood parasites or in which extrapair paternity occurs. In other bird species (e.g. dunnocks, *Prunella modularis* and alpine accentors, *Prunella collaris*) males use indirect cues, adjusting their parental care based on the amount of exclusive sexual access they had to the female, which correlates with degree of paternity[15,18].

Recognition by associative learning depends, like spatially based recognition, on a spatial and/or temporal component. However, the crucial difference is that during the period of association the animal learns the cues or labels that identify its putative kin and then uses those cues to recognize its kin outside of the association context.

Box 2. Kin recognition mechanisms

Recognition alleles: this mechanism requires that a gene (complex) confers an identifiable phenotype on its carrier, which also enables the carrier to perceive that phenotypic trait and discriminate accordingly[40]. An allele with these characteristics would be expected to spread more rapidly by natural selection through a population than other alleles without this discriminatory capacity.

Phenotype matching: kin recognition through phenotype matching involves the learning and assessment of phenotypes (e.g. song) of particular individuals. An individual's phenotype, or that of closely related conspecifics, forms a phenotypic 'template' against which the phenotypes of unfamiliar individuals can be compared. The degree of matching reflects kinship, enabling appropriate kin-directed behaviour.

Associative learning: this is a widespread mechanism for discriminating kin from non-kin[41] and is probably effective in any situation where there is a reliable correlation between genetic relatedness and association. Imprinting of offspring onto parents or vice versa, where recognition results from a period of association, is an obvious manifestation of this mechanism. The requirement of a period for familiarization with relatives is likely to be satisfied in any species with an extended period of parental care.

Spatially based recognition: this is probably the simplest mechanism of kin recognition and one for which there is good evidence among birds. When relatives are predictably distributed in space, location can offer an accurate and consistent cue to genetic relatedness. For example, breeders providing parental care to offspring may use a simple rule: 'feed anything in my nest or territory'.

Kin recognition in avian societies

What evidence is there for the various mechanisms of kin recognition among cooperative breeders? Typical cooperative breeding systems, with helpers at the nest, are characterized by natal philopatry and an extended period of association with kin on a family territory[19]. In most cases, kin-directed helping precedes dispersal and independent breeding. In this situation, a decision rule 'care for any offspring in my natal territory' could serve as a reliable discriminator between kin and non-kin. However, the longer the helpers remain on their natal territory the higher the probability that there will be some turnover of breeders with a subsequent diminution of relatedness to the helped brood. In theory, recognition through association avoids this problem, provided that breeder turnover occurs outside a putative 'associative-learning period'.

There have been no published experimental studies of kin recognition among cooperative species, and little attention has been paid to the actual cues used by helpers when making helping decisions. Just two studies have explicitly addressed the question of how kin discrimination is achieved by helpers. Helping behaviour by Galapagos mockingbirds (*Nesomimus parvulus*) sometimes occurs among non-kin, and the care of helpers is better predicted by prior association than by kinship *per se*[20]. Similarly, in the Seychelles warbler (*Acrocephalus sechellensis*) the helping rule is based on the identity of parents and helpers rather than that of nestlings, and a rule such as 'help anyone who fed me as a nestling' is the best predictor of care[21]. Thus, helpers always

feed the broods of their parents, but not of their siblings, even when the relatedness of nestlings to helpers is identical. Given that benefits of helping other kin are available, one might not expect such a restrictive discrimination rule. However, the presence of more than one brood with identical relatedness of nestlings to potential helpers is extremely rare and, under these circumstances, it might be impossible for more powerful discrimination rules to evolve. However, it is clear that such a rule cannot be universal because in other cooperative species, such as in long-tailed tits (*Aegithalos caudatus*)[22], care for the offspring of siblings from the same brood is the typical pattern. Therefore, although current evidence suggests that recognition through association and/or familiarity is the most likely mechanism for kin discrimination among cooperatively breeding birds, it appears that the precise rule of thumb will vary from species to species.

Among cooperative breeders, there is no evidence that kin-directed helping behaviour ever occurs when there are no opportunities to learn the phenotypic characters of kin. It seems likely that helpers use visual or auditory cues to discriminate between familiar and unfamiliar individuals. However, this does not mean that associative learning is the only possible mechanism; indeed, all four mechanisms are not mutually exclusive. In small families of cooperating birds, recognition of specific individuals can be relatively straightforward, but it might be a greater cognitive challenge for larger family groups [e.g. groups of white-winged chough (*Corcorax melanorhamphos*) may comprise up to 18 birds]. In large groups, a 'generic' cue might be more appropriate. For example, in newly formed long-term but noncooperative flocks of black-capped chickadees (*Parus atricapillus*), individuals converge on a flock-specific call over a few weeks[23]. If such convergence was typical of cooperative groups, a mechanism of associative learning and/or phenotype matching could be used for the discrimination of kin from non-kin.

There are limitations to associative learning as a recognition mechanism. First, any non-kin in the right place during the 'associative-learning period' will be regarded as kin, and true kin who are absent will be regarded as non-kin. In cooperative breeders, the likelihood of perceiving non-kin as kin might be reduced by a conditional rule requiring not simply association, but also the investment of care (i.e. 'help anyone who fed me as a nestling'). Such a rule might appear as reciprocal cooperative behaviour.

The second limitation is that in some avian societies with extensive networks of kin of varying relatedness [e.g. the noisy miner (*Manorina melanocephala*)[24] and the white-fronted bee-eater (*Merops bullockoides*)[25]] finer discrimination might pay. A simple learning rule based on association might not enable helpers to discriminate between close kin and distant kin. One of the outstanding questions in such complex societies is the extent of reproductive sharing; that is, how closely matched are genealogy and genetic relatedness? In those species where reproduction is shared among several family members, such as the acorn woodpecker (*Melanerpes formicivorus*)[26], and even with nonfamily members, such as superb fairy wrens (*Malurus cyaneus*)[27], recognition through association can offer only approximate information on kinship.

The third limitation is that if familiarity arises through provisioning of nestlings or fledglings by helpers, there is a risk that the mechanism of associative learning can be exploited by cheats, a phenomenon dubbed 'kinship deceit'[28]. For example, in the white-winged chough, an obligate cooperative breeder in which reproductive success is positively related to group size, groups kidnap unrelated fledglings. Kidnapped young who survive subsequently become unrelated helpers in their adoptive groups[29]. However, even when helpers usually gain indirect fitness benefits through helping, the resulting selection against care for non-kin could weaken if significant direct fitness benefits are gained by helping.

Potential helpers will be selected to employ recognition mechanisms that result in an optimal balance between two kinds of error: helping non-kin recipients and rejecting kin as recipients[6]. A cautious strategy with a high recognition threshold might avoid giving care to all non-kin, but might also result in care not being given to kin. A generous strategy with a low recognition threshold might ensure that all kin are recognized and helped, but might also result in frequent care for non-kin. The frequency and cost of errors in a recognition system will depend on the fitness benefit of discrimination, which in turn is likely to be a function of the ecology and life history of the species. In those species where indirect fitness gains are the major fitness benefit of helping, the fitness cost will be small if occasional care for non-kin by helpers resulting from recognition errors occurs at low frequency. An alternative explanation, and one that is likely to apply widely, is that there are also direct fitness benefits of helping, so apparent errors might not be maladaptive. Indeed, in most species for which sufficient data are available, it appears that direct fitness gains play an important role in the evolution and/or maintenance of cooperation[19]. In only two species, white-fronted bee-eaters and the primary helpers of pied kingfishers (*Ceryle rudis*), are direct fitness benefits thought to be absent[30,31]. Selection for error-free kin recognition will be weaker in the presence of direct fitness benefits through cooperation.

The role of kin recognition in the evolution of cooperative breeding

The crucial question is which of the four kin discrimination mechanisms (Box 2) is sufficiently reliable to permit the evolution of cooperative breeding in those species where kin selection is an important factor. It is perhaps surprising that so little attention has been paid to the question of how kin discrimination is achieved among cooperative breeders. Historically, the emphasis of research in this field has focused on the ecological basis for natal philopatry (why delay dispersal?) and the fitness benefits of helping among offspring that have 'stayed at home' (why help?) (Box 3). A better knowledge of the mechanism of kin recognition and discrimination will contribute to our understanding of both issues. Generally, cooperative systems tend to be characterized by a long period of close association before helping, relative to non-cooperative systems, enabling helpers to

Box 3. Consistency of ecological constraints model for cooperative breeding

The ecological constraints model proposes that delayed dispersal occurs when constraints (such as high predation or a shortage of suitable habitat or mates) cause dispersal costs to outweigh the costs of deferred independent reproduction (e.g. Ref. 42). This model has successfully explained the occurrence of natal philopatry at the species level[19], but has been less successful in explaining why some species, but not others, should have evolved cooperation. Comparative studies of cooperative and noncooperative species have generally failed to identify consistent ecological correlates of cooperative breeding[43–46]. This lack of interspecific support for the constraints hypothesis might be because constraints on preferred-breeding options are ubiquitous among birds, as shown by the widespread occurrence of nonbreeding 'floaters' in most bird populations[47]. Furthermore, deferred reproduction and continuous association with kin need not be a prerequisite for cooperation. In white-fronted bee-eaters (*Merops bullockoides*) and European bee-eaters (*M. apiaster*), some birds become helpers only after failing in their own independent breeding attempt[25,48], and in the long-tailed tit (*Aegithalos caudatus*) all helpers who have failed to reproduce successfully are exbreeders[22,49]. In these three species, helpers accrue indirect fitness benefits by directing care towards kin, and there is also a period of close association of relatives either at the breeding colony or in family flocks prior to independent breeding (i.e. there is still an opportunity to learn the identity of kin).

direct care towards kin with a high degree of confidence (Box 3). If recognition through associative learning is the usual mechanism of kin discrimination, comparative studies that focus on the timing of natal dispersal and the opportunity for familiarity to develop could reveal important but hitherto elusive differences between cooperative and noncooperative species. This does not imply that cooperation is an inevitable consequence of long associations and familiarity. For example, in Siberian jays (*Perisoreus infaustus*), grown offspring stay at home on the natal territory with their parents for a year or more as nonbreeders but do not assist their parents in caring for offspring[32].

Is an extended period of association essential for cooperation to evolve among kin? The fact that offspring recognition appears to be widespread among birds suggests that a long-term association (i.e. more than a few weeks of dependence) might not be necessary to learn individual identities. However, little (if anything) is known of the persistence of parent–offspring recognition beyond the point of independence. There is also an important distinction to be drawn between parent and offspring recognition. In noncooperative species, offspring might gain little selective advantage by discriminating parents from nonparents, whereas in cooperative species this ability could be critical to the development of families.

Finally, as already mentioned, any recognition system is unlikely to be error-free. The frequency with which such errors occur depends on the roles of indirect and direct fitness benefits in the maintenance of helping behaviour. But, as in other fields of evolutionary biology, it is clear that it is essential to study underlying mechanisms if we are to fully understand the limits of adaptive behaviour.

Conclusions and future work

Current evidence suggests that associative learning is the most likely mechanism of kin recognition enabling helpers to discriminate kin from non-kin in avian societies. However, despite the significance of such mechanisms for the evolution and maintenance of cooperative breeding systems, there is a distinct lack of empirical studies in this area. In particular, we highlight three potentially very interesting avenues of investigation. First, experimental studies of: (1) the putative 'associative-learning period'; (2) how good recognition mechanisms are at enabling fine discrimination between close and distant kin of similar familiarity; (3) whether generic or individual cues are employed in kin recognition; and (4) how recognition ability varies at different stages of a species' life history.

Second, studies of kin recognition that include both simultaneous and sequential discrimination tests should reveal more about the cues used to discriminate kin from non-kin. In particular, investigation of whether such cues and the ability to discriminate accordingly are fixed in space and time. For example, the recognition threshold might vary according to the selection pressure to recognize kin.

Finally, we suggest that comparative studies of kin recognition and discrimination in cooperative and noncooperative species would be worthwhile.

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References

1 Stacey, P.B. and Koenig, W.D. (1990) *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior*, Cambridge University Press
2 Emlen, S.T. (1997) **Predicting family dynamics in social vertebrates,** in *Behavioural Ecology: an Evolutionary Approach* (Krebs, J.R. and Davies, N.B., eds), pp. 228–253, Cambridge University Press
3 Walters, J.R. (1990) **Red-cockaded woodpeckers: a 'primitive' cooperative breeder,** in *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (Stacey, P.B. and Koenig, W.D., eds), pp. 69–101, Cambridge University Press
4 Rabenold, K.N. (1985) **Cooperation in breeding by non-reproductive wrens: kinship, reciprocity and demography,** *Behav. Ecol. Sociobiol.* 17, 1–17
5 Piper, W.H. and Slater, G. (1993) **Polyandry and incest avoidance in the cooperative stripe-backed wren of Venezuela,** *Behaviour* 124, 227–247
6 Sherman, P.W., Reeve, H.K. and Pfennig, D.W. (1997) **Recognition systems,** in *Behavioural Ecology: an Evolutionary Approach* (Krebs, J.R. and Davies, N.B., eds), pp. 69–96, Blackwell
7 Beecher, M.D., Beecher, I.M. and Hahn, S. (1981) **Parent–offspring recognition in bank swallows. II. Development and acoustic basis,** *Anim. Behav.* 29, 95–101
8 Davies, L.S. and McCaffrey, F.T. (1989) **Recognition and parental investment in Adelie penguins,** *Emu* 89, 155–158
9 Hepper, P.G. (1991) *Kin Recognition*, Cambridge University Press
10 Shugart, G.W. (1977) **The development of chick recognition by adult Caspian terns,** *Proc. Colonial Waterbird Group* 1, 110–117
11 Beecher, M.D. (1981) **Development of parent–offspring recognition in birds,** in *Development of Perception* (Aslin, R.K., Alberts, J.R. and Peterson, M.R., eds), pp. 45–66, Academic Press
12 Beecher, M.D. (1991) **Successes and failures of parent–offspring recognition,** in *Kin Recognition* (Hepper, P.G., ed.), pp. 94–124, Cambridge University Press
13 Halpin, Z.T. (1991) **Kin recognition cues of vertebrates,** in *Kin Recognition* (Hepper, P.G., ed.), pp. 220–258, Cambridge University Press
14 Beecher, M.D. (1988) **Kin recognition in birds,** *Behav. Genet.* 18, 465–482
15 Davies, N.B. *et al.* (1992) **Paternity and parental effort in dunnocks *Prunella modularis*: how good are male chick-feeding rules?** *Anim. Behav.* 43, 729–745
16 Pagel, M.D. (1997) **Desperately concealing father: a theory of parent–infant resemblance,** *Anim. Behav.* 53, 973–981
17 Bateson, P.P.G. (1982) **Preferences for cousins in Japanese quail,** *Nature* 295, 236–237
18 Hartley, I.R. *et al.* (1995) **The polygynandrous mating system of the alpine accentor, *Prunella collaris*. II. Multiple paternity and parental effort,** *Anim. Behav.* 49, 789–803
19 Emlen, S.T. (1991) **Evolution of cooperative breeding in birds and mammals,** in *Behavioural Ecology: an Evolutionary Approach* (Krebs, J.R. and Davies, N.B., eds), pp. 301–337, Blackwell
20 Curry, R.L. and Grant, P.R. (1990) **Galapagos mockingbirds: territorial cooperative breeding in a climatically variable environment,** in *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (Stacey, P.B. and Koenig, W.D., eds), pp. 289–332, Cambridge University Press
21 Komdeur, J. (1994) **The effect of kinship on helping in the cooperative breeding Seychelles warbler (*Acrocephalus sechellensis*),** *Proc. R. Soc. London Ser. B* 256, 47–52
22 Glen, N.W. and Perrins, C.M. (1988) **Cooperative breeding by long-tailed tits,** *Br. Birds* 81, 630–641
23 Nowicki, S. (1989) **Vocal plasticity in captive black-capped chickadees: the acoustic basis and rate of call convergence,** *Anim. Behav.* 37, 64–73
24 Dow, D.D. and Whitmore, M.J. (1990) **Noisy miners: variations on the theme of communality,** in *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (Stacey, P.B. and Koenig, W.D., eds), pp. 559–592, Cambridge University Press
25 Emlen, S.T. (1990) **White-fronted bee-eaters: helping in a colonially nesting species,** in *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (Stacey, P.B. and Koenig, W.D., eds), pp. 487–526, Cambridge University Press
26 Koenig, W.D. and Mumme, R.L. (1987) *Population Ecology of the Cooperatively Breeding Acorn Woodpecker*, Princeton University Press
27 Mulder, R.A. *et al.* (1994) **Helpers liberate female fairy-wrens from constraints on extra-pair mate choice,** *Proc. R. Soc. London Ser. B* 255, 223–229
28 Connor, R.C. and Curry, R.L. (1995) **Helping non-relatives: a role for deceit?** *Anim. Behav.* 49, 389–393
29 Heinsohn, R.G. (1991) **Kidnapping and reciprocity in cooperatively breeding white-winged choughs,** *Anim. Behav.* 41, 1097–1110

30 Emlen, S.T. and Wrege, P.H. (1988) **The role of kinship in helping decisions among white-fronted bee-eaters,** *Behav. Ecol. Sociobiol.* 23, 305–315

31 Reyer, H-U. (1984) **Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*),** *Anim. Behav.* 32, 1163–1178

32 Ekman, J., Sklepkovych, B. and Tegelstorm, H. (1994) **Offspring retention in the Siberian jay (*Perisoreus infaustus*): the prolonged brood-care hypothesis,** *Behav. Ecol.* 5, 245–253

33 Curry, R.L. (1988) **Influence of kinship on helping behavior in Galapagos mockingbirds,** *Behav. Ecol. Sociobiol.* 22, 141–152

34 Clarke, M.F. (1984) **Co-operative breeding by the Australian bell miner, *Manorina melanophrys* Latham: a test of kin selection theory,** *Behav. Ecol. Sociobiol.* 14, 137–146

35 Clarke, M.F. (1989) **The pattern of helping in the bell miner *Manorina melanophrys*,** *Ethology* 80, 292–306

36 Marzluff, J.M. and Balda, R.P. (1990) **Pinyon jays: making the best of a bad situation by helping,** in *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (Stacey, P.B. and Koenig, W.D., eds), pp. 197–237, Cambridge University Press

37 Brown, J.L. and Brown, E.R. (1990) **Mexican jays: uncooperative breeding,** in *Cooperative Breeding in Birds: Long-term studies of Ecology and Behavior* (Stacey, P.B. and Koenig, W.D., eds), pp. 267–288, Cambridge University Press

38 Mumme, R.L. (1992) **Do helpers increase reproductive success? An experimental analysis in the Florida scrub jay,** *Behav. Ecol. Sociobiol.* 31, 319–328

39 Shugart, G.W. (1987) **Individual clutch recognition by Caspian terns, *Sterna caspia*,** *Anim. Behav.* 35, 1563–1565

40 Hamilton, W.D. (1964) **The genetical evolution of social behaviour. I,** *J. Theor. Biol.* 7, 1–16

41 Blaustein, A.R., Bekoff, M. and Daniels, T.J. (1987) **Kin recognition in vertebrates (excluding primates): empirical evidence,** in *Kin Recognition in Animals* (Fletcher, D.J.C. and Michener, C.D., eds), pp. 287–331, John Wiley & Sons

42 Stacey, P. and Ligon, J.D. (1991) **The benefits of philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effect,** *Am. Nat.* 137, 831–846

43 Dow, D.D. (1980) **Communally breeding Australian birds with an analysis of distributional and environmental factors,** *Emu* 80, 121–140

44 Ford, H.A. *et al.* (1988) **The relationship between ecology and the incidence of cooperative breeding in Australian birds,** *Behav. Ecol. Sociobiol.* 22, 239–249

45 Du Plessis, M.A., Siegfried, W.R. and Armstrong, A.J. (1995) **Ecological and life-history correlates of cooperative breeding in South African birds,** *Oecologia* 102, 180–188

46 Poiani, A. and Pagel, M. (1997) **Evolution of avian cooperative breeding: comparative tests of the nest predation hypothesis,** *Evolution* 51, 226–240

47 Newton, I. (1992) **Experiments on the limitation of bird numbers by territorial behaviour,** *Biol. Rev.* 67, 129–173

48 Lessells, C.M. (1990) **Helpers at the nest in European bee-eaters: who helps and why?** in *Population Biology of Passerine Birds. An Integrated Approach* (Blondel, J. *et al.*, eds), pp. 357–368, Springer-Verlag

49 Hatchwell, B.J. and Russell, A.F. (1996) **Provisioning rules in cooperatively breeding long-tailed tits *Aegithalos caudatus*: an experimental study,** *Proc. R. Soc. London Ser. B* 263, 83–88

Extinction risk in the sea

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Jean Baptiste de Lamarck and Thomas Huxley, two of the foremost thinkers of the 18th and 19th centuries, believed that humanity could not cause the extinction of marine species. Their opinions reflected a widespread belief that the seas were an inexhaustible source of food and wealth of which people could barely use a fraction. Such views were given weight by the abundant fisheries of the time. Additionally, the incredible fecundity and wide distributions of marine fishes, combined with limited exploitation, provided ample justification for optimism. The ideas of Huxley and Lamarck persist to this day, despite a sea change in the scale and depth of our influence on the oceans. Marine species could be at a far greater risk of extinction than we have assumed.

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There is no doubt about the growing magnitude of human impact on the oceans. More than half of the world's population live within 60 km of the coast, and the figure could reach 75% by the year 2020 (Ref. 1). Collapsed fisheries have become commonplace and we are beginning to appreciate that the impacts of fishing extend far beyond the species we target[2]. Approximately 95% of marine fish catches come from continental shelf regions, where fisheries now consume an estimated 24–35% of primary production[3]. Coastal waters are becoming increasingly polluted, and there is a large-scale loss of coastal wetland habitat. It is in these same coastal waters that most known marine biodiversity resides[4].

Despite this evidence of human influence, most marine scientists probably still share the views of Lamarck and Huxley, that although we might be able to deplete populations of marine species, we cannot cause their extinction. Lamarck put it succinctly in the early 19th century: 'Animals living in the waters, especially the sea waters are protected from the destruction of their species by Man. Their multiplication is so rapid and their means of evading pursuit or traps are so great that there is no likelihood of his being able to destroy the entire species of any of these animals' (*Philosophie Zoologique*, 1809). Huxley, in his 1883 address to the International Fisheries Exhibition in London, reinforced the point in relation to the rapidly industrializing fisheries of the time, stating 'Any tendency to over-fishing will meet with its natural check in the diminution of the supply, …this check will always come into operation long before anything like permanent exhaustion has occurred.'

We surveyed 235 scientists from among those most likely to appreciate the possibility of extinction in the sea. Fourteen of the 45 who replied did not think that marine species were at serious risk of extinction. We think that this faith in the resilience of marine species is misplaced, that there might already have been numerous extinctions in recent times that we have simply failed to notice, and that the coming decades are likely to see many more.

Evidence for contemporary marine extinctions

Steller's sea cow (*Hydrodamalis gigas*), the Caribbean monk seal (*Monachus tropicalis*) and the great auk (*Pinguinis impennis*) are long gone, victims of relentless exploitation. But these were air-breathing animals that spent time on land, an exceptional lifestyle compared with most marine species. Until recently, there has been only one well documented

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